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A GILL-INHABITING NEW GENUS AND SPECIES OF THE BRANCHIOBDELLIDA (ANNELIDA: CLITELLATA)

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Abstract.—Holt, Perry C., Department of Biology and Center for Systematics Collections, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.—*Adenodrilus hemophagus*, from Douglas County, Oregon, U.S.A., is described, its affinities discussed, and evidence of its way of life presented.

The first formally described branchiobdellid, *Branchiobdella astaci* Odier, 1823, apparently is an inhabitant of the gill chambers of the host (Odier, 1823:75). Though there is little doubt that some European branchiobdellids are adapted to life in branchial chambers, the taxonomy of European branchiobdellids appears to be in a state of confusion. Pop (1965) was undoubtedly correct in reducing many specific names to synonymy, but I doubt that there are only four species of branchiobdellids in Europe and I have no idea how many are true ectoparasites that feed on the host's branchiae.

In Asia, Yamaguchi (1934:216) reported that two species of "*Stephanodrilus*" (= *Cirrodrilus*) are found in the gill chambers of the host and two others of this genus are found in both the gill chambers and on the body surface.

The knowledge of the gill-inhabiting branchiobdellids of North America is almost as scanty. *Bdellodrilus illuminatus* (Moore, 1893) is common and known to live in the branchial chambers and feed on the blood of the host sucked from filaments of the gills. *Cambarincola branchiophilus* Holt, 1954, also inhabits the gill chambers of crayfishes and some species, e.g., *Cambarincola demissus* Hoffman, 1963, are suspected of doing so. No effort to study gill-inhabiting branchiobdellids as such has been undertaken. In part, this is because the method of collecting, satisfactory for those worms that live on the exposed surfaces of the host, is not so good for the branchial forms; they tend to be excessively shrunken and contorted by the alcohol-formalin fixative I use. In addition the usual method of preparing the animals for study (dehydrating in alcohol, clearing in clove oil and mounting in balsam) exacerbates this difficulty.

The specimens described herein, nonetheless, were prepared by these methods and, with the aid of dissections, a satisfactory account of their structure was made possible. In other respects, my usual methods were used (Holt, 1960), and all drawings are oriented with the anterior of the animal or part thereof to the reader's right.

It seems appropriate, therefore, to call attention to this population of branchiobdellids, representing a new genus, from Douglas County, Oregon, since previous records of gill-inhabiting North American branchiobdellids are so few.

I wish to acknowledge the aid of my wife and daughter in collecting; Dr. Horton H. Hobbs, Jr., for identifying the hosts; Dr. Marian Pettibone for her many kindnesses in cataloging type-specimens and reviewing manuscripts.

Adenodrilus, new genus

Type-species.—*Adenodrilus hemophagus*, here designated.

Diagnosis.—Relatively large worms, unpaired anterior nephridiopore; body terete; body-wall muscles thin; head markedly less in diameter than body segments; sucker subequal to head in diameter; peristomium entire to faintly lobed; jaws triangular with prominent lateral flanges; spermiducal gland with vasa deferentia entering ectad to ental end, often expanded; no prostrate or prostatic protuberance; ejaculatory duct long, thick, heavily muscular; bursa elongate pyriform; penis muscular; spermatheca with spermathecal bursa, long ectal duct, expanded bulb, long glandular ental process.

Etymology.—*Adenos*, G., gland and *drilos*, G.—"gland-worm."

Affinities.—The most recent attempt to develop a scheme of relationships among branchiobdellid genera (Holt, 1969) was proposed rather timidly and the discovery of *Adenodrilus* increases the difficulties of devising satisfactory theories of phylogenetic relationships within the order. For now, I can only postulate that the adaptive radiation of the group occurred early in its history and that considerable parallelism or convergence or both characterized its course. The best that can be done is to briefly consider a few genera that share important features with *Adenodrilus*.

Four genera were placed in the *Cirrodrilus*-lineage (Holt, 1969:197) and *Adenodrilus* fits nicely with these (*Cirrodrilus* Pierontoni, 1905; *Branchiobdella* Odier, 1823; *Xironogiton* Ellis, 1919; *Ankyrodrilus* Holt, 1965) except that all have two anterior nephridiopores. *Cronodrilus* Holt, 1968b, possesses only one anterior nephridiopore and the vasa deferentia enter the spermiducal gland ectad to its ental end as in *Adenodrilus*. But the penis of the latter is muscular, instead of the eversible, non-cellular, cuticular, tubular one of *Cronodrilus* and is doubtfully eversible (see below). Among the genera characterized by a spermiducal gland in which the vasa deferentia enter the gland ectad to its ental end, *Cirrodrilus* appears to be most

nearly similar to *Adenodrilus*. Indeed, except for the two anterior nephridiopores of *Cirrodrilus inukaii* (Yamaguchi, 1934) and the different structure of the jaws, *C. inukaii* and the species of *Adenodrilus* described below could be considered as congeneric.

Yamaguchi (1934 and previous papers) did not designate a type-species for his genus "*Stephanodrilus*" (= *Cirrodrilus* Pierantoni 1905). But both *C. inukaii* (the only species adequately illustrated) and *C. cirratus* have unpaired anterior nephridiopores. *Adenodrilus*, thus, shares only two important features, the manner of entry of the vasa deferentia into the spermiducal gland and the basic structure of the bursa and penis with *Cirrodrilus*. So, the unexpected combination of an unpaired anterior nephridiopore and an ectal entry of the vasa deferentia into the spermiducal gland, leaves me with only one dubious choice in an attempt to place *Adenodrilus* in my former scheme (Holt, 1969: Figure 2). It seems to belong to the group composed of *Cronodrilus* and *Bdellodrilus* Moore, 1895, except for its muscular and possibly non-eversible penis and, on the assumption that muscular, protrusible penes have evolved from eversible, cuticular ones several times in the radiation of the branchiobdellids, I must, for now, leave *Adenodrilus* there.

Geographical and other remarks.—No great significance should be attached to the geographical location of *Adenodrilus*. I have previously commented upon the relationships of the American and Asian branchiobdellid faunas (Holt, 1968a; 1969) and postulated an ancient origin for the genera of the order (Holt, 1968a; 1969; 1977). The discovery of *Adenodrilus* is only one of several additional bits of evidence supporting these speculations.

So little is known of the ecology, physiology, feeding habits, etc., of the branchiobdellids, that the basis of my assertion that *A. hemophagus* feeds on blood drawn from the host's gills, in the absence of direct observation, requires comment. There is a recognizable parasitic facies common to the truly gill-inhabiting, blood-sucking species. In *Bdellodrilus illuminatus* and *Adenodrilus hemophagus* the body-wall is thin and the glandular elements of the body-wall and the sucker, by virtue of the reduction of the musculature, accentuated. The coelomic spaces seem proportionately greater in volume. The gut is filled with a liquid. These characteristics of gill-inhabiting branchiobdellids account for the difficulties of preparing specimens for study by the usual methods. And it is on the basis of this "parasitic facies" and the invariable presence within the gut of specimens of *A. hemophagus* of a clear fluid coagulum without detritus of any sort or the remains of any other animals whatsoever that I am confident of the habitat on the host and the food of *A. hemophagus*: the branchial chambers and the blood of the hosts.

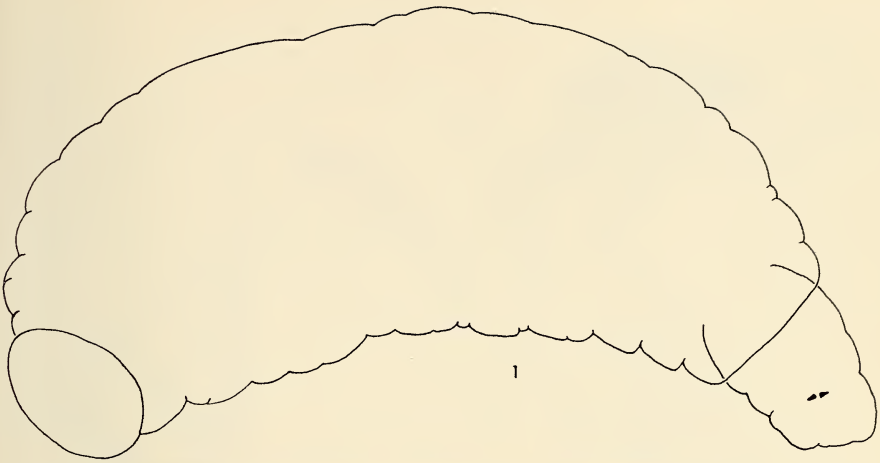

Fig. 1. *Adenodrilus hemophagus*: Lateral view of holotype.

Adenodrilus hemophagus, new species
Figs. 1–5

Type-specimens.—Holotype, USNM (Smithsonian Institution) 54640, 16 paratypes, PCH 1333 (VPI & SU Center for Systematics Collections), from *Pacifastacus leniusculus klamathensis* (Stimpson, 1857) taken from Elk Creek, Douglas Co., Oregon, at junction of State Road 231 and U.S. Highway 99, 20.3 km SW of Cottage Grove, by Perry C. and Virgie F. Holt, 11 July 1960.

Diagnosis.—As for the genus.

Etymology.—*Hemos*, G., blood, and *phagos*, G., eater.

Description.—Specimens of *A. hemophagus* are relatively large branchiobdellid worms. The holotype has the following approximate dimensions (in mm): *total length*, 5.0; *greatest diameter*, 1.2; *head length*, 0.7; *head diameter*, 0.5; *diameter, segment I*, 0.5; *diameter sucker*, 0.6. Five paratypes, selected at random, have the following approximate average dimensions (ranges given in parentheses): *total length*, 5.2 (4.0–6.6); *greatest diameter*, 1.1 (1.0–1.1); *head length*, 0.7 (0.6–0.8); *head diameter*, 0.4 (0.4–0.5); *diameter, segment I*, 0.5 (0.5–0.6); *diameter, sucker*, 0.5 (0.5–0.5). These animals are remarkably uniform in size. Most are bent in preservation into a semicircle and the variation in total length is probably an artifact of the difficulty of obtaining precise measurements with an ocular micrometer.

The worms have a corpulent appearance; anterior and posterior portions are noticeably less in diameter than the mid-part of the body (Fig. 1). The body wall is remarkably thin, the longitudinal musculature is sparse and

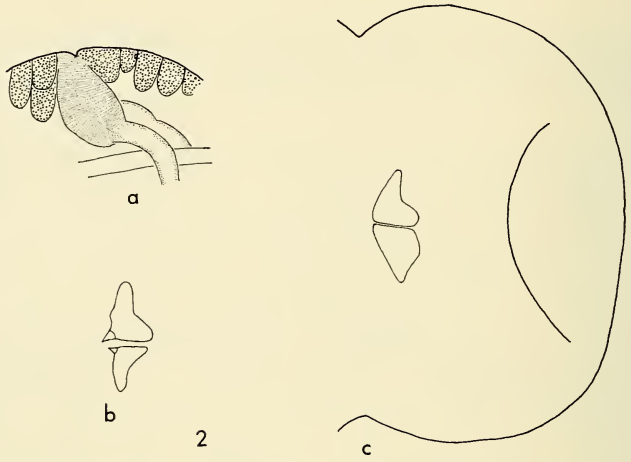

Fig. 2. *Adenodrilus hemophagus*: a, Optical section through anterior nephridiopore; b, Lateral view of jaws; c, Peristomium, from specimen without peristomial lobes. From paratypes.

its individual cells slender. The glandular components of the epidermis are prominent by virtue of the paucity of muscles, including those of the clitellar region (segments VI and VII). The sucker, contrary to the usual branchiobdellid condition, lacks a specialized musculature; instead it is provided with a cluster of about a dozen large unicellular glands whose ducts discharge onto its concave surface.

The head is marked externally by one annular sulcus in addition to the peristomial one. The lips of the peristomium are usually marked by indistinct indentations into 4 upper and 2 lower lobes, but the peristomium may appear entire (Fig. 2c). Internally, there is one pharyngeal sulcus. There are no oral papillae. The anterior nephridiopore (Fig. 2a) is unpaired and the nephridial outlet duct is surrounded by densely granular cells.

The body is often completely flexed into a circle in preservation, making observation of internal structures very difficult, a difficulty increased by the density of the spermatozoa which fill segments V and VI. The overall facies of the animals is a parasitic one.

The gut is expanded, as usual, in segments III–IX, its expansion in segment VIII extends into segment IX. The gut is filled throughout its length with a homogeneous, non-particulate, fluid. The ganglia of the nervous system are proportionately small; the major blood vessels proportionately large.

The jaws are prominent, medium dark brown, triangular in lateral aspect, but in actuality essentially U-shaped in frontal view, with large lateral flanges. Each jaw is equipped with a prominent median tooth; no lateral

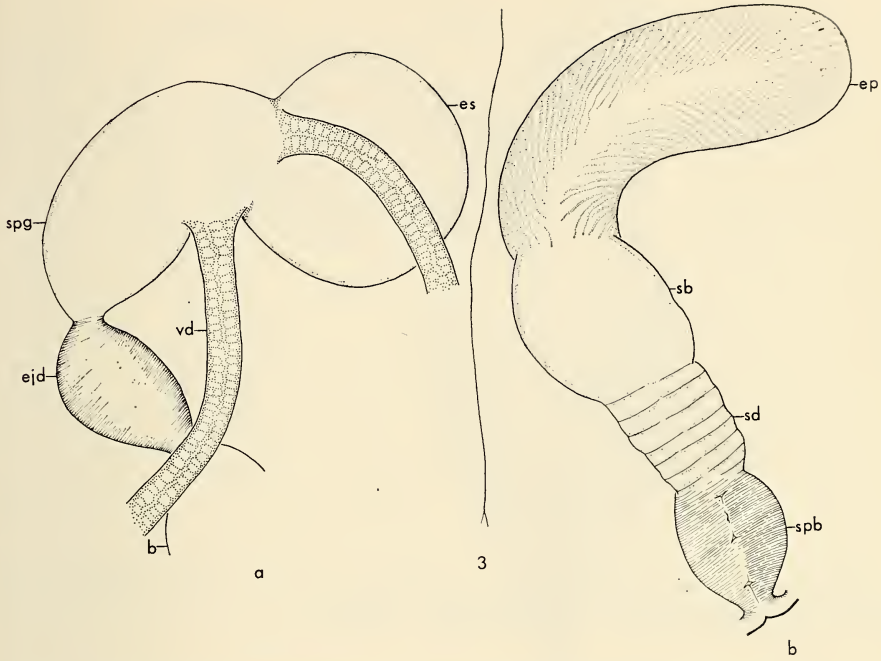

Fig. 3. *Adenodrilus hemophagus*: a, Latero-dorsal view of male reproductive system; b, Same of spermatheca. From a paratype. Abbreviations: b, bursa; ejd, ejaculatory duct; ep, ental processes of spermatheca; es, ental end of spermiducal gland; sb, spermathecal bulb; sd, spermathecal ectal duct; spb, spermathecal bursa; spg, spermiducal gland; vd, posterior vas deferens.

teeth were observed. The dental formula is, then, the somewhat rare one of 1/1 (Fig. 2b).

The vasa deferentia are thick and enter the spermiducal gland at about ⅓ the length of the latter ectad to its ental end. The spermiducal gland is often constricted (Fig. 3a; 4a) at the point of entry of the vasa deferentia and tapers ectally to its junction with the ejaculatory duct. It appears in 2 forms which are presumably dependent upon the reproductive state of the animal. Often it is rather slender, with a thick glandulo-muscular wall and with spermatozoa present in its lumen (Fig. 5). In other cases, it is greatly extended, filled with a clear fluid, and spermatozoa are absent or difficult to detect (Fig. 3a).

The ejaculatory duct is unusual. Subequal to the bursa in length, it appears to be composed of 3 layers of muscles: inner and outer longitudinal ones and an inner circular one (Fig. 5). Its structure suggests that it is capable of a strong pumping action.

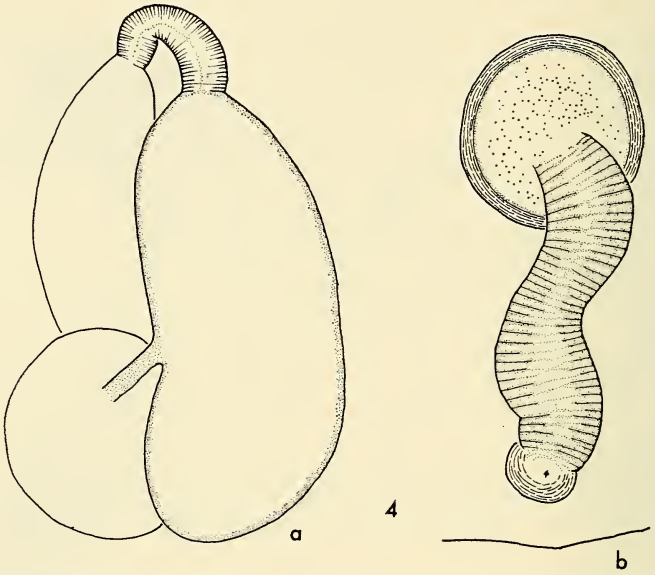

Fig. 4. *Adenodrilus hemophagus*: a, Dorso-lateral view of male reproductive system; b, Ventro-lateral view of spermatheca. Paratypes.

The bursa is elongated pyriform in shape, broadest at the juncture of its penial sheath region and the bursal atrium. The atrium constitutes about ⅔ of the organ and its walls taper to a narrow outlet duct. The penis is composed of dense muscle and hence, by analogy with species with similar penes, is protrusible. But in the absence of direct observation, this conclusion is uncertain: the lumen of the penis, though obscure, is a meandering canal enclosed in the muscles of the organ and is undoubtedly longer than the retracted penis, suggesting that the penis is eversible (Fig. 5). The total size of the male reproductive organs is, proportionate to the diameter of the segment in which they lie, rather small; they extend dorsad about ⅕ of the distance to the dorsum of the body.

The spermatheca is clearly differentiated into 4 distinct regions (Fig. 3b). Ectally, there is a spermathecal bursa with heavily muscular walls and a lumen expanded to form a cavity remarkably similar to the atrium of the male bursa. This is followed by a spermathecal duct with a wall composed of rather thin bands of muscle cells and a wide lumen. The wall of the spermathecal bulb is relatively thin but ensheathed in muscle, the lumen expanded as expected, but, surprisingly often with little evidence of stored spermatozoa within it. The spermatheca ends entally in a long prominent ental process, though the organ often is bent in such wise that

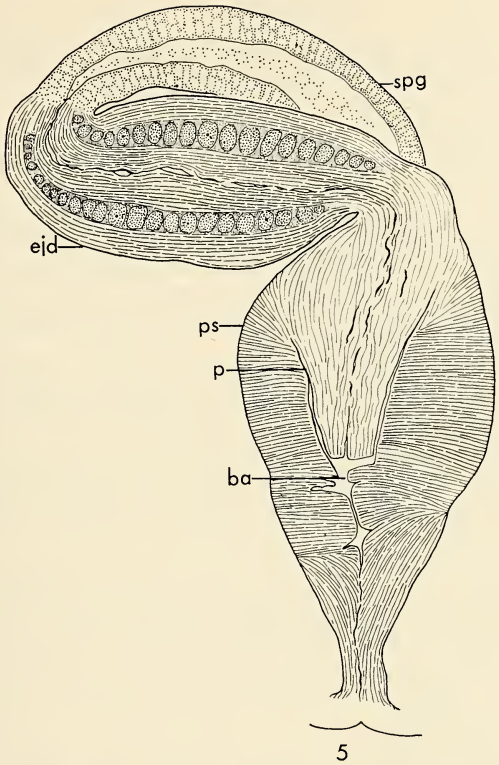

Fig. 5. *Adenodrilus hemophagus*: Detail (schematic) of part of male reproductive system. Abbreviations: ba, bursal atrium; ejd, ejaculatory duct; p, penis; ps, penial sheath of bursa; spg, spermiducal gland. Paratype.

the ental process is obscured (Fig. 4b). The inner wall of the ental process is composed of glandular cells, each with a long process extending to almost the center of the lumen (Fig. 3b).

Variations.—The absence of lobes of the lips in some specimens, the remarkable differences in the degree of distension of the spermiducal gland and the various positions in which the reproductive organs may lie have been noted and to some extent illustrated: a somewhat unusual range of variations, but the overall correlation of parts among the specimens studied, leaves no doubt as to the conspecificity of these worms.

Affinities.—As for the genus.

Host.—*Pacifastacus leniusculus klamathensis* (Stimpson, 1857).

Distribution.—Known only from the type-locality.

Material examined.—The type-series.

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